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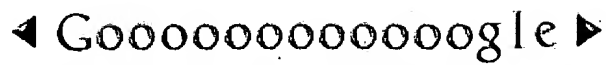
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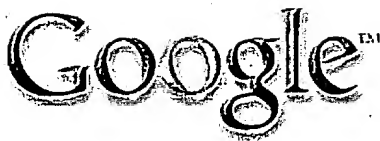
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Alterations in gastric mucin synthesis by *Helicobacter pylori*

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INTRODUCTION

Helicobacter pylori is recognized as a cause of chronic active gastritis, gastric and duodenal ulcers, and gastric cancer, though the mechanisms of pathogenesis for *H.pylori*-associated diseases are not yet well understood [1-4]. The ecological niche to which *H.pylori* is well-adapted is the mucous layer of the human gastric antrum, which has **mucin** glycoproteins as major constituents. Mucins, high-molecular weight carbohydrate-rich glycoproteins that coat the surface of the stomach and are secreted into the lumen, function to protect the stomach and could be important in *H.pylori* colonization. For further understanding the pathogenesis of *H.pylori* related diseases, it is important to consider whether *H.pylori* colonization of the surface epithelium is associated, as cause or effect, with changes in the gastric **mucin** synthesized by surface mucous cells.

MUCINS PRODUCED IN NORMAL STOMACH

The entire gastrointestinal tract is coated with a protective mucous layer. The main components of the viscoelastic mucous are **mucin** glycoproteins. Mucins are thought to protect the surface of the gastrointestinal tract from mechanical damage, from dessication, and from chemical irritants. Gastric mucins are the major components of an unstirred mucous-bicarbonate layer that protects the gastric epithelium from the high concentrations of acid in the stomach lumen and from autodigestion by pepsin. The protective functions of the gastric mucous layer imposes rigid requirements on the structure of gastric mucins (Figure 1). They must be very high in molecular weight and highly hydrated to provide the viscoelasticity necessary for protection from mechanical damage, and must also be acid-stable and have little non-glycosylated polypeptide exposed as a target for pepsin.

Figure 1 Models of gastric **mucin** structure. Lower bars represent cDNA sequences of MUC1 cell-surface **mucin** and MUC5AC secreted **mucin**, with different domains labeled. Resulting structures of the proteins with attached carbohydrate are schematically represented above.

Like mucins from a number of sources, human gastric mucins are very high in molecular weight and are heavily substituted with O-linked oligosaccharides. Human mucins are encoded by at least nine distinct **mucin** genes, of which three, MUC1, MUC5AC, and MUC6, are expressed at high levels in the normal stomach (Table 1).

MUC1 **mucin** is well characterized [5]. The protein encoded by the MUC1 gene has a large central domain (VNTR, Variable Number of Tandem Repeats) composed of a variable number (25 to 125) of tandem repeats of a 20-amino acid sequence with 25% **threonine** and serine and 7% proline. Unlike most other mucins, the MUC1-encoded protein has a transmembrane segment and a cytoplasmic tail that can interact with the cytoskeleton. The O-linked carbohydrates on MUC1 **mucin** are heterogeneous, differ between tumors and normal epithelial cells [6], and can influence the recognition

of the **mucin** protein by different monoclonal antibodies. MUC1 **mucin** is produced to some extent by most epithelial cells, but has been studied most extensively in mammary, pancreatic, and colon cancer cells.

MUC5AC is expressed in the stomach and in tracheobronchial cells. Immunohistochemical studies indicate that MUC5AC apomucin is present in surface mucous cells of the gastric epithelium [7,8]. MUC5AC **mucin** has a small tandem repeat sequence of 8 amino acids, interspersed with cysteine-containing regions (Figure 1). The glycoprotein is very large with the bulk of the molecule made up of heavily glycosylated tandem repeats of an 8-amino acid peptide sequence rich in threonine (to which O-linked oligosaccharides are attached) and proline. Interspersed irregularly within the tandem repeat region are cysteine-containing motifs. Like MUC2 intestinal **mucin**, both the N-terminal and the C-terminal have cysteine-rich globular domains [9] with sequence similarity to the D domains of pre-pro-von Willebrand factor and an inferred cystine-knot motif, topologically similar to epidermal growth factor (EGF). The cysteine-rich globular domains of secreted mucins may be involved in the oligomerization of **mucin** or in binding to collagen of basement membranes [10]. MUC5AC is expressed in the normal stomach, but not in normal colon. Aberrant expression of MUC5AC has been reported, however, in colorectal cancers and adenomas [8,11,12] and may be related to the progression of colon cancers.

MUC6 is also expressed in the normal stomach, but in mucous glands rather than surface mucous cells [7,8,13,14]. This **mucin** has a very large tandem repeat sequence of 169 amino acids, very high in amounts of Thr, Ser, and Pro [13]. The high content of Thr and Ser likely accounts for the large amount of carbohydrate present on this molecule. Thus, there are (at least) two completely different secreted mucins produced by the normal stomach. How these mucins differ in carbohydrate (and whether they differ in function) is speculative. Genes for both MUC5AC and MUC6 have been assigned to a region of chromosome 11 that also codes for two other secretory mucins [15], with a gene order of HRAS-MUC6-MUC2-MUC5AC-MUC5B-IGF2.

Like mucins from other sources, the carbohydrate portion of gastric **mucin** is heterogeneous. Several neutral oligosaccharide structures have been published [16,17], but the overall complement of oligosaccharides is not known. The results of histochemical studies suggest that the carbohydrate portion of the **mucin** in surface mucous cells is different from that in mucous glands. The surface mucous cells are stained by PAS, while mucous glands (cardiac gland, mucous neck cells, and pyloric gland cells) are stained by alcian blue. The "neutral" mucins in surface mucous cells are also stained by galactose oxidase/Schiff, suggesting the presence of terminal Gal or GalNAc [18]. The mucous gland cells uniquely show periodate-enhanced binding of concanavalin A, called paradoxical ConA staining. The structural basis for this is unclear, but it may detect terminal alpha-GlcNAc [18]. The mucous gel layer covering the surface epithelium has been shown to have clearly demarcated layers of two distinct **mucin** types [19]. On the basis of staining properties, these likely correspond to the surface-type neutral **mucin** (MUC5AC) reactive with galactose oxidase and to the gland-type acid **mucin** (MUC6), possibly sulfomucin, revealed by periodate-enhanced (paradoxical) ConA staining.

EFFECT OF *H.PYLORI* ON GASTRIC MUCIN IN VIVO

Though both the thickness and the hydrophobicity of the mucous gel layer is decreased in the gastric mucosa of ulcer patients [20], it has not been established whether this is associated with increased **mucin** degradation, decreased **mucin** synthesis, or a change in **mucin** type. It has been postulated that one important pathogenic property of *H.pylori* is its ability to weaken the mucous gel that protects the gastric epithelium [21,22], but the presence or absence of mucinase activities in *H.pylori* is controversial [23-25]. Direct analysis of mucins from *H.pylori* infected and uninfected patients show no decrease in viscosity, arguing against *H.pylori* dependent mucin degradation [26]. In spite of histochemical observations of mucous depletion accompanying *H.pylori* infection, qualitative alterations in the type of **mucin** produced have only recently been studied.

In order to determine the effect of *H.pylori* infection on **mucin** gene expression in the gastric epithelium [7], biopsies from *H.pylori*-positive and *H.pylori* negative patients were examined by immunohistochemistry (Table 2). MUC6 was limited to mucous glands of *H.pylori* negative patients, but 72% of *H.pylori* positive patients also expressed MUC6 on surface mucous cells. In contrast, MUC5AC **mucin** was seen in significantly fewer surface mucous cells of *H.pylori*-positive specimens. Overall, the percent of the surface epithelium stained by anti-MUC5 was significantly lower in *H.pylori*-positive specimens than in *H.pylori*-negative specimens ($P < 0.01$). Carbohydrates recognized by LeX and paradoxical ConA staining were aberrantly expressed in the surface mucous cells of 16/27 and 17/23 of *H.pylori*-positive tissues, respectively. There was a suggestive but non-significant decrease in staining for MUC1 **mucin**. Retrospective examination of clinical histories and histological findings showed that the **mucin** alterations occur in *H.pylori* infected individuals with and without ulcers, but not in patients with non-*H.pylori*-associated gastritis or gastric ulcers (Figure 2). This indicates that the mucin alterations are not simply a secondary effect of inflammation.

For more direct examination of **mucin** gene expression, the presence of MUC5AC and MUC6 message in antral biopsies were examined by *in situ* hybridization [7]. In antral biopsy specimens from *H.pylori*-negative patients, MUC5AC mRNA was homogeneously expressed in surface epithelial cells. MUC5AC expression in the surface epithelial cells of *H.pylori*-positive patients was patchy, however, and often absent from large areas of the surface epithelium. Concordance between the pattern of MUC5AC expression as determined by *in situ* hybridization and immunohistochemistry was 100%. MUC6 expression was limited to cells of the deep glands in *H.pylori*-negative patients, seen by both *in situ* hybridization and immunohistochemistry. In contrast, 6 of 8 *H.pylori*-positive specimens

Table 1 Human mucin genes

Gene	Locus	mRNA size	Tandem Repeats	Other structural features	Expression in normal tissues

MUC1	1q21-24	4-7 kb	20 AA	Transmembrane	Most epithelia
MUC2	11p15.5	14-16 kb	23 AA, -16 AA	D-domains, cystine knot	Colon>small intestine>respiratory tract
MUC3	7q22	16-17.5 kb	17 AA, 59 AA	Cystine knot	Small intestine>colon, gall bladder
MUC4	3q29	16.5-24 kb	16 AA		Respiratory tract, cervix>GI tract
MUC5AC	11p15.5	17-18 kb	8 AA	D-domains, cystine knot	Stomach (surface)>respiratory tract
MUC5B	11p15.5	17.5 kb	29 AA, interrupted	D-domains, cystine knot	Respiratory tract, salivary gland, cervix>GI tract
MUC6	11p15.5	16.5-18 kb	169 AA	Cystine knot	Stomach (glands), gall bladder
MUC7	4	2.4 kb	23 AA	No homology to large mucins	Salivary glands
MUC8	12q24.3	-9 kb	18 AA, 41 AA	Not Thr/Ser rich	Trachea

Table 2 Histochemical staining of mucins in gastric biopsy specimens

Antigen		<i>H.pylori</i> negative	<i>H.pylori</i> positive
MUC5AC	% Stained ^{*a} , intensity score (surface)	(69.8±3.5)%, 2.8±0.1	(51.2±5.7)%, 2.6±0.1
MUC6	% Stained ^{**a} , intensity score (surface) ^a	4%, 0.1±0.1	72%, 1.8±0.2
Le\+b	% Stained ^{**a} , intensity score (surface) ^a	63%, 0.9±0.2	96%, 1.9±0.2
Paradoxical ConA	% Stained ^{**a} , intensity score (surface) ^a	18%, 0.4±0.2	79%, 2.1±0.3
LeX	% Stained ^{**a} , intensity score (surface) ^a	4%, 0.4±0.4	59%, 1.0±0.2
MUC1	Intensity score (surface), intensity score (glands)	2.6±0.2, 1.7±0.1	2.7±0.1, 1.4±0.2
Sialyl Tn	Intensity score (surface), intensity score (glands) ^a	1.8±0.2, 1.9±0.1	1.6±0.1, 1.4±0.1

*% of surface epithelium stained; ** % of patients with surface staining; ^a*P*<0.05, *H.pylori* positive vs *H.pylori* negative

Figure 2 Expression of MUC5AC in surface epithelium of normal human stomach and gastritis and gastric ulcer specimens. ^a*P*<0.05 vs corresponding *H. pylori* negative group.

(0/7 *H.pylori* negative specimens) had focal MUC6 mRNA expression in surface epithelial cells. MUC5AC and MUC6 gene expression were examined in antral biopsies obtained from patients with *H.pylori*-associated antral gastritis (biopsy-proven) before and after documented eradication of the bacterium. In 7 of 10 cases MUC5AC expression increased (*P*=0.004) after *H.pylori* eradication (Figure 3). Eradication of *H.pylori* also resulted in reversal of MUC6 antigen expression toward normal patterns.

The effect of *H.pylori* on gastric mucin expression was further examined by purification and immunochemical analysis of mucins from gastric juice of *H. pylori* positive and *H.pylori*-negative patients. For *H.pylori*-infected patients and uninfected patients that had been examined for immunohistochemical staining of biopsy tissues, gastric

Figure 3 MUC5 expression in patients before and after eradication of *H.pylori* infection. MUC5 gene expression was determined by *in situ* hybridization. Bars show mean percent of epithelial cells expressing MUC5. Lines show changes in MUC5AC expression in individual patients.

aspirates were used as a source for mucin purification by gel filtration and CsCl density gradient centrifugation. There was no significant difference in yield of mucin or carbohydrate content between *H.pylori*-positive and *H.pylori* negative specimens (Figure 4). The purified mucins were examined by ELISA for MUC6 and Le-b antigenic activity. MUC6 activity was higher (*P*=0.026) in mucins from the *H.pylori*-infected patients than in mucins from uninfected patients. Mucins from the *H.pylori*-infected patients also bound monoclonal antibody to Le-b antigen to a significantly greater extent (*P*=0.014) than mucins from the uninfected patients (Figure 4). Subsequently, these purified mucins have been examined by SDS-PAGE and Western analysis. Infection with *H.pylori* was associated with an increase in MUC6 (detected with anti-M6P and also with anti-Le-b and Ulex europea agglutinin) and a decrease in MUC5AC (detected with anti-M5P and 45M1 antibodies and also with peanut agglutinin and Vicia villosa agglutinin) in these secreted mucins.

Figure 4 Purification and analysis of mucins from gastric juice. Upper left, yield of mucins purified from gastric aspirates of 5 *H. pylori*-negative and 5 *H. pylori*-positive patients. Upper right, carbohydrate content of purified mucins. Lower left, binding of antibody to MUC6 peptide in ELISA. Lower right, binding of antibody to Lewis-b antigen.

These results establish that there is aberrant surface expression of gland-type gastric **mucin** in surface mucous cells of *H. pylori* infected patients, accompanied by focally decreased MUC5AC **mucin**. This decrease in MUC5AC **mucin** and aberrant expression of MUC6 might be expected to disrupt the protective surface mucin layer. How or whether alterations in gastric mucins would influence processes that lead to disease is an important question which requires that the specificity and mechanisms of **mucin** depletion be better understood.

EFFECT OF *H. PYLORI* ON MUCIN SYNTHESIS IN VITRO

Analyses of tissue specimens and purified **mucin** glycoproteins indicate that gastric surface-type **mucin** expression is reversibly decreased in *H. pylori*-infected patients [7] but do not allow direct examination of **mucin synthesis**. Gastric cells in culture were examined to determine the effect of *H. pylori* on **mucin synthesis** [27]. KATO III gastric epithelial cells were incubated in the presence or absence of *H. pylori*, and the **mucin** produced was quantitated by labeling with [³H] glucosamine and size exclusion HPLC on Superose 6 columns. The ³H-labeled high-molecular weight glycoprotein was confirmed to be **mucin** by CsCl density gradient centrifugation, chemical and enzymatic degradation treatments. *H. pylori* (type strain NCTC11637), under conditions that had little effect on viability, inhibited the **synthesis** of **mucin** by 82% (Figure 5). There was no inhibition of **mucin synthesis** by the non-gastric pathogen *Campylobacter jejuni*, and little inhibition by a strain (Tx30a) of *H. pylori* that is CagA-negative and non-toxigenic. Similar results were seen in five other gastric cell lines tested (Figure 5). Inhibition of **mucin synthesis** was detected as early as 4 h after addition of bacteria, and was partially reversible, though with a slower time-course than the onset of inhibition. Inhibition of **mucin** labeling was concentration dependent (Figure 6) and did not require the presence of intact bacteria. There was no inhibition by a soluble extract of *H. pylori*, but the *H. pylori* pellet fraction gave inhibition equivalent to intact bacteria.

Figure 5 Effect of *H. pylori* on **mucin synthesis** in six gastric cell lines. Cells were labeled 22 h with [³H] glucosamine in the presence or absence of 1 OD600 *H. pylori*, and labeled glycoproteins were analyzed by size-exclusion HPLC.

In a pulse-chase analysis, *H. pylori* had no effect on **mucin** secretion. Furthermore, there was little or no degradation of mature **mucin** in the presence or absence of *H. pylori*. Further experiments, to examine the effects of *H. pylori* on **mucin** glycosylation, used benzyl-GalNAc, which specifically inhibits **synthesis** of peripheral carbohydrate on **mucin**-type glycoproteins [28].

Incubation of KATO III with *H. pylori* decreased labeling of **mucin** to a similar extent in the presence or absence of benzyl-GalNAc (Figure 7), indicating that the effect of *H. pylori* is not due to inhibition of peripheral glycosylation *per se*, but results from inhibition of **synthesis** of **mucin** core structures.

Figure 6 Inhibition of **mucin synthesis** by subfractions of *H. pylori*. KATO III cells were labeled with [³H] glucosamine in the presence of different concentrations of intact *H. pylori* (open circles), *H. pylori* lysate (filled circles), the 100,000×g pellet (open triangles), or the 100,000×g supernatant (open squares).

Figure 7 Effect of *H. pylori* on **synthesis** of peripheral and core carbohydrate structures of **mucin**. KATO III cells were incubated with or without 2 mmol/L benzyl-GalNAc, and labeled for 4 h in the presence or absence of 1 OD600 *H. pylori*. Bars show void volume (V₀) containing labeled **mucin**. Solid areas show labeling of the peripheral carbohydrate (inhibitable by benzyl-GalNAc). Open areas show residual labeling of core structures in the presence of benzyl-GalNAc.

KATO III produces MUC5AC and MUC1 mucins, and the amount of both **mucin** proteins is decreased by co-incubation with *H. pylori* (Figure 8). Expression of another high molecular weight glycoprotein, CEA, and another control protein, galectin-3, was unaffected by *H. pylori*. *H. pylori* also decreased the amount of MUC5AC protein in BGC-823 gastric cells and the amount of MUC1 protein in the BGC-823, AGS, and MGC 80-3 cell lines. The inhibition of **synthesis** of both MUC5AC and MUC1 protein was concentration dependent and associated with the insoluble fraction of *H. pylori* lysates. Kinetically, the onset of inhibition of MUC1 expression was more rapid than inhibition of MUC5AC expression. MUC1 inhibition was seen within 4 h while MUC5AC inhibition was slower. MUC1 recovery was also more rapid than recovery of

Figure 8 Effect of *H. pylori* on expression of MUC1 and MUC5AC in KATO III gastric epithelial cells *in vitro*. KATO III cells were incubated with or without *H. pylori*, and cell lysates were subjected to Western analysis. Content of MUC1 antigen, detected with monoclonal antibody HMFG2, and of MUC5AC antigen, detected with monoclonal antibody CLH2, is expressed as percentage of untreated cells.

MUC5AC.

These experiments [27] demonstrate that *H. pylori* decreases the amount of total **mucin**, and MUC5AC and MUC1 proteins in gastric epithelial cells. Indirect evidence indicates that this is due to a decrease in the **synthesis** of mucin protein rather than changes in glycosylation, secretion, or degradation of mucins. These results may help to explain the **mucin** depletion associated with *H. pylori* infection *in vivo* [7,29].

INFLUENCE OF MUCINS ON *H. PYLORI* ADHESION

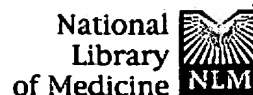
Most of the *H. pylori* in the stomach are present in the mucus gel layer, and appear to cause little harm to the host; adhesion of *H. pylori* to the gastric epithelial cell surface may be required for causing disease. For example, induction of the proinflammatory chemokine interleukin-8, requires that bacteria be in contact with the epithelial cell surface [30,31]. **Mucin** glycoproteins produced by the gastric epithelial surface could influence the process of *H. pylori* adhesion in two ways: First, secreted glycoproteins could bind to bacterial adhesins and help to keep the bacteria in the mucous gel layer, preventing their approach to the epithelium. Although *H. pylori* has several different adhesins which could be involved in binding to mucins [32-35] and human gastric **mucin** has been shown to inhibit bacterial binding to other cell types, e.g., erythrocytes and HEp-2 cells [36,37], it is not known whether secreted gastric **mucin** can inhibit the adhesion of *H. pylori* to gastric epithelial cells. Second, cell-surface **mucin** glycoproteins could shield the epithelial cell surface from exposure to contact-dependent virulence factors, preventing a adhesion-dependent **synthesis** of pro-inflammatory chemokines. In MUC1-expressing cells, the highly glycosylated tandem repeat domain extending out from the cell surface can interfere with cell-cell interactions, for example, integrin-mediated aggregation [38]. Since adhesion of *H. pylori* to gastric epithelial cells requires their close proximity to the cell surface where they can interact with integrins or other cell-surface receptors, cell-surface mucins might be expected to block adhesion of *H. pylori* to gastric epithelial cells.

Since previous results indicated that gastric surface type mucins are decreased by *H. pylori* both *in vivo* [7] and *in vitro* [27], we sought to determine the influence of **mucin** on adhesion of *H. pylori* to cultured gastric epithelial cells. For measurement of the adhesion of *H. pylori* to gastric epithelial cells, an assay was established using biotinylated *H. pylori*, with bacteria attached to the BGC-823 gastric epithelial cells quantitated with avidin-biotin-peroxidase complex and ABTS as chromogen. The binding of bacteria was characterized with regard to time dependence, temperature dependence, and bacterial strain dependence. Optimal conditions for adhesion were found to be 30 min incubation at 37°C. Under conditions where the CagA/cytotoxin positive type strain of *H. pylori*, NCTC 16137, bound well to BGC-823 cells, there was little binding of the CagA-negative, cytotoxin-negative strain of *H. pylori*, Tx30a or of the non-human pathogen *Helicobacter mustelae*. As further validation, the standard binding assay was compared to colony counts for detection of viable *H. pylori* bound to BGC-823 cells (Figure 9). Binding of biotinylated bacteria was equivalent to binding of viable bacteria.

Figure 9 Assay of adhesion of *H. pylori* to gastric epithelial cells. Biotin-labeled *H. pylori* were incubated with BGC-823 cells for 30 min at 37°C, and attached bacteria were quantitated using the avidin-biotin-complex assay (A, left panel) or by colony counts (B, right panel).

BGC-823 cells are well differentiated, attach well to tissue culture plastic, and are susceptible to *H. pylori*-dependent inhibition of **mucin** synthesis [27,39]. In comparison to other gastric epithelial cell lines, there was more binding of *H. pylori* to BGC-823 cells (which produces MUC5AC **mucin** and has relatively low levels of MUC1 cell-surface **mucin**) than to two cell lines (AGS and MGC-803) which do not produce MUC5AC **mucin** but produce high levels of MUC1 **mucin** [27,40]. This inverse correlation between MUC1 expression and *H. pylori* adhesion in gastric epithelial cell lines suggests that MUC1 mucin could interfere with *H. pylori* adhesion.

In order to test the role of **mucin** in *H. pylori* adhesion, we sought to inhibit **mucin**

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